

# Primate origins: plugging the gaps

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Recent discoveries of fossil primate specimens have produced several surprises and challenged prevailing views of early primate evolution. Plesiadapiforms, long regarded as 'archaic primates', may perhaps be linked to the peculiar colugos instead. Inferred relationships of the earliest known undoubted primates (adapids and omomyids) are in turmoil. Both groups have been proposed as sources for the simian primates. Although the origin of the simian primates is obscure, new fossil evidence could push it further back by at least 10 million years. Such uncertainties reflect the low sampling level of the primate fossil record, which can potentially also lead to underestimation of times of origin within the primate tree.

A PICTURE of the earliest phases of primate evolution that seemed broadly acceptable just a decade ago has been increasingly challenged. Several recent discoveries of early fossil primates have opened up new possibilities for the pattern and timing of emergence of the main groups of primates between the late Cretaceous and the end of the Eocene. As part of the upheaval, the cohesion of various fossil groups as monophyletic units has also been questioned. Widespread acceptance of the essentially Palaeocene Plesiadapiformes ('archaic primates') as a well defined group of exclusive early relatives of primates has been shaken by new fossil evidence and analyses. Certain features have been interpreted as indications that some genera, at least, may instead be directly linked to the Dermoptera (gliding colugos, also called 'flying lemurs'). New fossil specimens, especially postcranial parts, of early Tertiary Adapidae ('lemuroids') have increasingly confirmed that some European genera (*Adapis*, *Leptadapis* and relatives) belong to a distinct sideline relative to other European genera (for example *Europolemur*, *Pronycticebus*), which are morphologically closer to North American adapids (for example *Notharctus*, *Smilodectes*). A revived suggestion that simian primates (monkeys, apes and humans) may be derived from the Adapidae directly conflicts with an alternative interpretation that the early Tertiary Omomyidae ('tarsioids') are relatives of tarsiers and simians whereas adapids are specific allies of modern lemurs and lorises (strepsirhine primates). Yet the discovery of several skulls of the North American omomyid *Shoshonius* led to the opposing claim that this genus is in fact even more directly linked to tarsiers, at the same time indicating a much earlier date for tarsier origins. Finally, dental evidence of the new genus *Algeripithecus* from a North African site dating back to the middle or even early Eocene would increase the age of the earliest yet identified simians by a striking margin of at least 10 million years. Given all this new fossil material and the sometimes conflicting interpretations that have been made, can the outlines of an emerging revised view of early primate evolution be traced? Consideration of the new evidence in the light of exploratory estimates of the current sampling level of the primate fossil record (Box 1) suggests that we may still have much to learn about the early relationships of primates and that inferred times of origin are likely to be pushed back much further into the past.

In 1979, when the last comprehensive review of fossil primates<sup>1</sup> was published, it seemed that broad agreement might be emerging with respect to the early evolutionary history of the primates (Fig. 1). It was almost universally accepted that the primates originated towards the close of the Cretaceous, just over 65 million years ago, and an overwhelming majority of primate palaeontologists regarded the Plesiadapiformes as members of the first major adaptive radiation from ancestral primates. Although these 'archaic primates' increasingly came to be seen

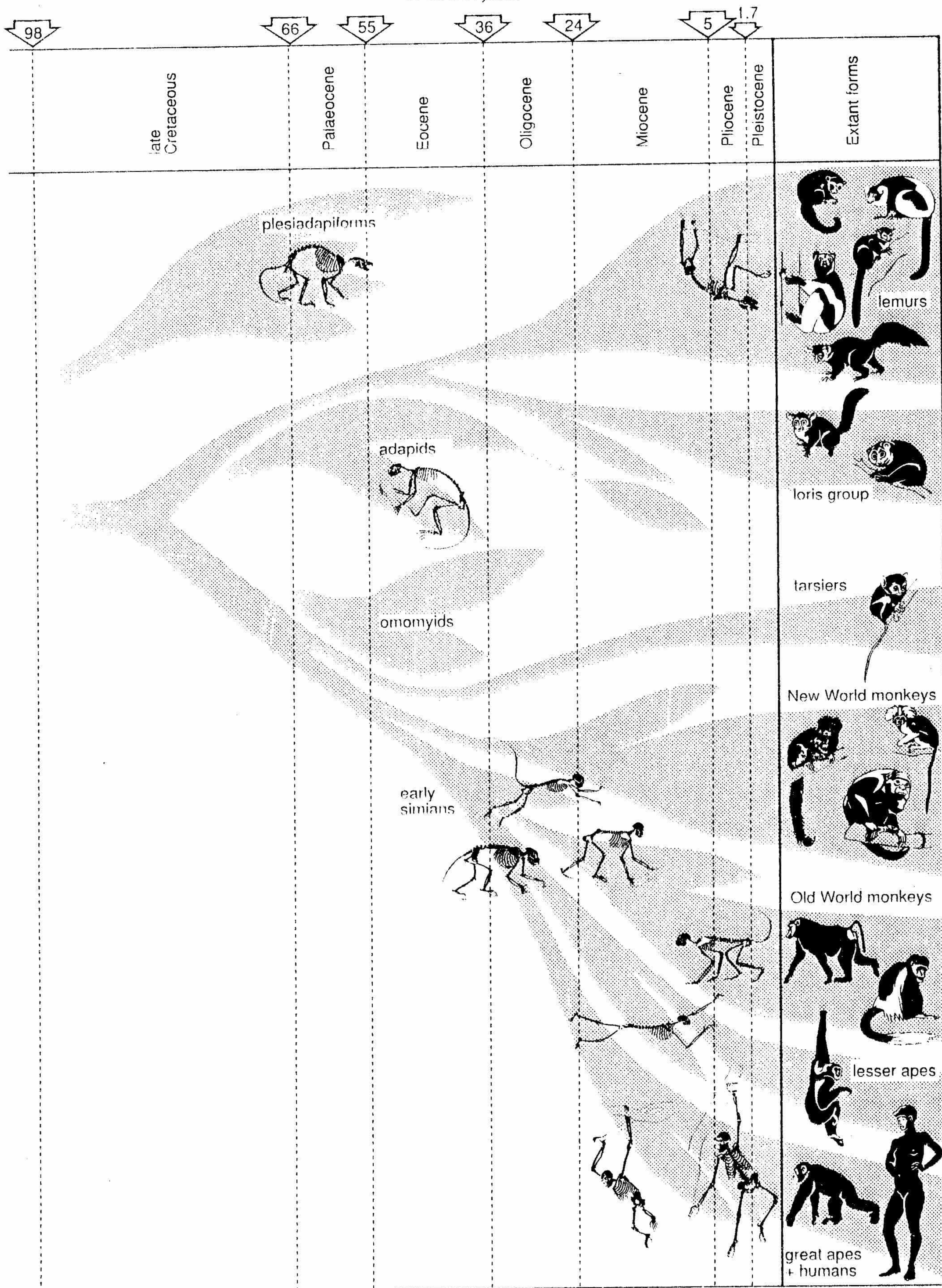
as a side branch, with no more than an early connection to the main radiation that led to modern primates, few doubted that the Plesiadapiformes were the exclusive sister group of primates of modern aspect ('euprimates'). There was also widespread, if not universal, agreement that the earliest known fossil primates of modern aspect from the Eocene fall into two distinct groups corresponding to the divergence of two main groups of living primates. The Adapidae were often regarded as relatives of the modern strepsirhine primates, whereas the Omomyidae were believed by many authors to be specifically allied to modern tarsiers. For the growing number of authors who accepted the existence of a haplorhine group containing tarsiers and simians, the omomyids almost automatically came to be seen as a key group close to the ancestry of all modern haplorhines.

Challenges to this picture of primate evolution have arisen in part because of new fossil material. But revised interpretations based on comparative studies and theoretical considerations have also contributed. In fact, exploration of the possible effects of a low sampling level on interpretations of the primate fossil record (Box 1) indicates that radical revision of prevailing views of primate evolution may be inevitable. Assessment of the possible effects of a low sampling level lead to certain predictions: (1) there is still enormous scope for the discovery of new fossil primate species; (2) with increased sampling of the primate fossil record, inferred times of origin are likely to increase, sometimes dramatically; (3) given the difficulties of interpreting fragmentary fossils, newly discovered specimens are likely to lead to repeated radical revision of inferred phylogenetic relationships; (4) the geographical context of primate evolution will also require reappraisal, as earlier times of origin necessarily imply different patterns of proximity between drifting continents.

## Relationships of Plesiadapiformes

The revolutionary proposal that some or all plesiadapiforms may be directly related to the modern colugo *Cynocephalus* rather than to primates of modern aspect<sup>2-4</sup> rests on two main lines of evidence. The first stems from a study of postcranial features by Beard<sup>5</sup>. The most striking inference, stimulated by new skeletal material, is that the hand of early Eocene *Phenacolemus* and *Ignaciuss* (both members of the family Paromomyidae) resembled that of *Cynocephalus*. For both *Phenacolemus* and *Ignaciuss*, the intermediate digital bones (phalanges) of each finger were reported to be longer than the basal phalanges, as in *Cynocephalus*, possibly indicating adaptation to support webbing between the fingers as part of a patagium (gliding membrane)<sup>2,6,7</sup>. Further, a cladistic analysis of the fossil evidence (based mainly on postcranial features) led to the conclusion that shared derived features link various plesiadapiforms more closely to colugos than to primates. Skeletons of *Plesiadapis*, however, do not seem to show any gliding adapta-

Millions of years



**BOX 1** How significant are gaps in the primate fossil record?

The fossil record of primate evolution is obviously incomplete, despite major continuing achievements by field palaeontologists. But how large are the gaps? Do we merely need to bridge over a few spaces here and there, or are there in fact yawning chasms? Our effectiveness in sampling past primate species has major implications for interpretations of primate evolution based on the known fossil record.

A crude estimate of our sampling level of the primate fossil record can be obtained relatively simply<sup>14,105</sup>. About 200 primate species exist today and it is widely accepted that the primates originated at least 65 Myr ago. To make a very rough calculation of the number of fossil primate species that have ever existed, it is necessary to make some assumption about the pattern of expansion of species numbers over time and to have an estimate of the average survival time for individual species. The simplest assumption for expansion of species numbers over time is a uniform rate of increase. If anything, this is likely to underestimate the numbers of extinct species, as it is commonly believed that the rate of speciation is initially high within a given group and then decelerates as available ecological niches become occupied. For fossil mammal species, several studies indicate that the average survival time is about 1 million years<sup>106</sup>. Taking all of these elements together, it is possible to infer that about 6,500 extinct primate species preceded the modern fauna.

This estimate can be used to assess our sample of the primate fossil record. Just over a decade ago, one review recognized 64 species of archaic primates and 186 fossil primates of modern aspect<sup>1</sup>. These 250 species represent 3.8% of the estimated total of past primate species. If the calculation is restricted to primates of modern aspect, commonly thought to have emerged about 55 Myr ago, the sampling level (186 out of an estimated total of 5,500 species) declines to only 3.4%. The potential implications of such low sampling levels for interpretation of the primate fossil record can be illustrated with a simple tree (Fig. 2). Although random distribution of discovery of fossil species within the tree is in fact unlikely, this does not affect the two main points that can be recognized. Firstly, times of origin for the group as a whole and for subgroups within the tree are likely to be considerably earlier than indicated by first known fossil representatives. It is common practice to date the time of origin of any group from just before the first known fossil representative, but this will obviously be seriously misleading at very low sampling levels. Indeed, some lineages within the tree may remain completely unrepresented in the known fossil record. This leads on to the second point that a very low sampling density may lead us to assign inappropriate ancestral positions to known fragmentary fossils.

Repeated simulations of the effects of different sampling levels for the tree shown in Fig. 2 yield average figures for the earliest fossil species that will be discovered within such a tree by chance and the correction factors required to infer the true time of origin of the group (Fig. 3). Preliminary calculations conducted by S. Tavaré (University of Southern California) have shown that the values derived by such simple simulation (Figs 2 and 3) are quite close to those that would be predicted using

branching process models, although some minor correction may be necessary. Such a simulation approach is admittedly approximate and any real tree is likely to show significant departures from the simple model. In many cases, however, sampling of the fossil record has been even poorer than assumed in the model. For example, primates of modern aspect are particularly well known from the Eocene: 83 of the 186 species mentioned above are derived from that epoch. During this exceptionally warm period, primates, characteristically inhabitants of tropical or subtropical forests, temporarily expanded from the south into the higher latitudes of the northern continents, where the probabilities of fossilization and subsequent fossil discovery were markedly higher. Because of significant geographic expansion, there may well have been a major bulge in species numbers within the primate tree during the Eocene, so a uniform model would underestimate the total number of extinct primate species.

For illustration, the derived correction factors can be applied to the known primate fossil record. With a sampling level of 3.8%, it is necessary to add a correction factor of about 30% to the time of origin indicated by the earliest known species. Hence, if archaic primates are accepted as genuine primates, an inferred time of origin of 65 Myr ago based on the first known representative would be revised to 85 Myr, well back in the Cretaceous. If the calculation is restricted to primates of modern aspect, the sampling level falls to 3.4%, requiring a correction factor of 33%, and a time of origin of 55 Myr ago based on the first known representative would be revised to 72 Myr, also a Cretaceous date.

There is, however, a further reason why the calculations illustrated in Figs 2 and 3 can be expected to underestimate the effects of a low sampling level for fossil primate species. An initial correction of the time of origin of primates of modern aspect based on the data in Fig. 3 yields a figure of 72 Myr. If, however, primates of modern aspect actually originated 72 Myr ago, rather than 55 Myr, the model in Fig. 2 yields a revised total of 7,200 extinct primate species. The sampling level for 186 known species correspondingly drops to 2.5%, which requires a correction factor of 40% instead of 33%, indicating an even earlier date of 77 Myr for the origin of primates. Serial recalculations of this kind eventually lead to a date of about 80 Myr for the origin of primates of modern aspect. A similar series of calculations can be applied to the simian primates, the earliest known fossil representative of which, until very recently, was dated at about 36 Myr, on the Eocene-Oligocene boundary. Application of a similar correction factor to this date would indicate an origin of simians at about 52 Myr, close to the Palaeocene-Eocene boundary.

It should also be noted that such recalculation of times of origin within the primate tree would have secondary implications for calibration of phylogenetic trees based on biomolecular data. Calibration has often been based on the suspect procedure of taking the date of the first known representative of a given group as close to the time of origin. Quite aside from other problems associated with biomolecular trees, it might be advisable to add 40% to all dates of divergence based on calibration derived from properly identified fossil evidence. □

tion. The second main source of evidence is a new, almost complete skull of *Ignacius*. Unlike primates of modern aspect, in which the auditory bulla grows out from the petrosal, the bulla of *Ignacius* can be confidently interpreted as the product of a separate entotympanic element (Fig. 4). As the presence of a petrosal bulla is generally regarded as a defining feature of primates, often stated to apply to plesiadapiforms as well, the entotympanic bulla of *Ignacius* sets paromomyids (at least) apart from primates. It has further been claimed that *Ignacius* specifically resembles colugos because the medial part of the

entotympanic bulla contacts the basioccipital on the underside of the skull, that the bulla in *Plesiadapis* may well be formed from an entotympanic as well, and that *Ignacius*, *Plesiadapis* and colugos also share an unusual secondary regression of the internal carotid system<sup>3</sup>. The inferred relationship between *Ignacius*, *Plesiadapis* and colugos was later reinforced by a cladistic analysis of 33 cranial features<sup>8</sup>.

Reassessment of the relationships of the Plesiadapiformes has been increasingly hampered by mounting evidence that the group may not be monophyletic. A recent major review, focused on dentitions, divided the Plesiadapiformes into two superfamilies: Microsyopoidea (families Microsyopidae and Palaeochthonidae) and Plesiadapoidea (families Plesiadapidae, Paromomyidae, Carpolestidae, Saxonellidae and Picrodontidae)<sup>9</sup>. The family Microsyopidae has had a chequered history, being sometimes excluded from the plesiadapiform group<sup>1,10</sup> and sometimes included<sup>11,12</sup>. Beard<sup>13</sup> omitted Microsyopidae, Palaeochthonidae and Picrodontidae from his analysis because of the lack of fossil evidence. For the remaining families, he proposed a new three-level arrangement for the order Dermoptera with colugos linked first to Paromomyidae, then to a group containing Plesiadapidae, Saxonellidae and Carpolestidae, and

FIG. 1 Outline tree showing the main groups of living primates and one possible interpretation of their relationships. The tree includes fossil forms known from relatively complete skeletons and emphasizes remaining gaps (for example, no fossil lemurs other than recent subfossils; no fossil tarsiers apart from a single lower molar from the Miocene<sup>117</sup>). Four key groups are discussed with respect to the early evolution of primates: plesiadapiforms; adapids; omomyids; early simians. Because of relatively low fossil sampling levels (Box 1), the time of origin of primates of modern aspect has been set at about 80 Myr ago, rather than at the value of 65 Myr often cited. The time of origin of simian primates has similarly been increased to about 55 Myr. (Adapted from ref. 14; illustration by Lukrezia Bieler-Beerli).

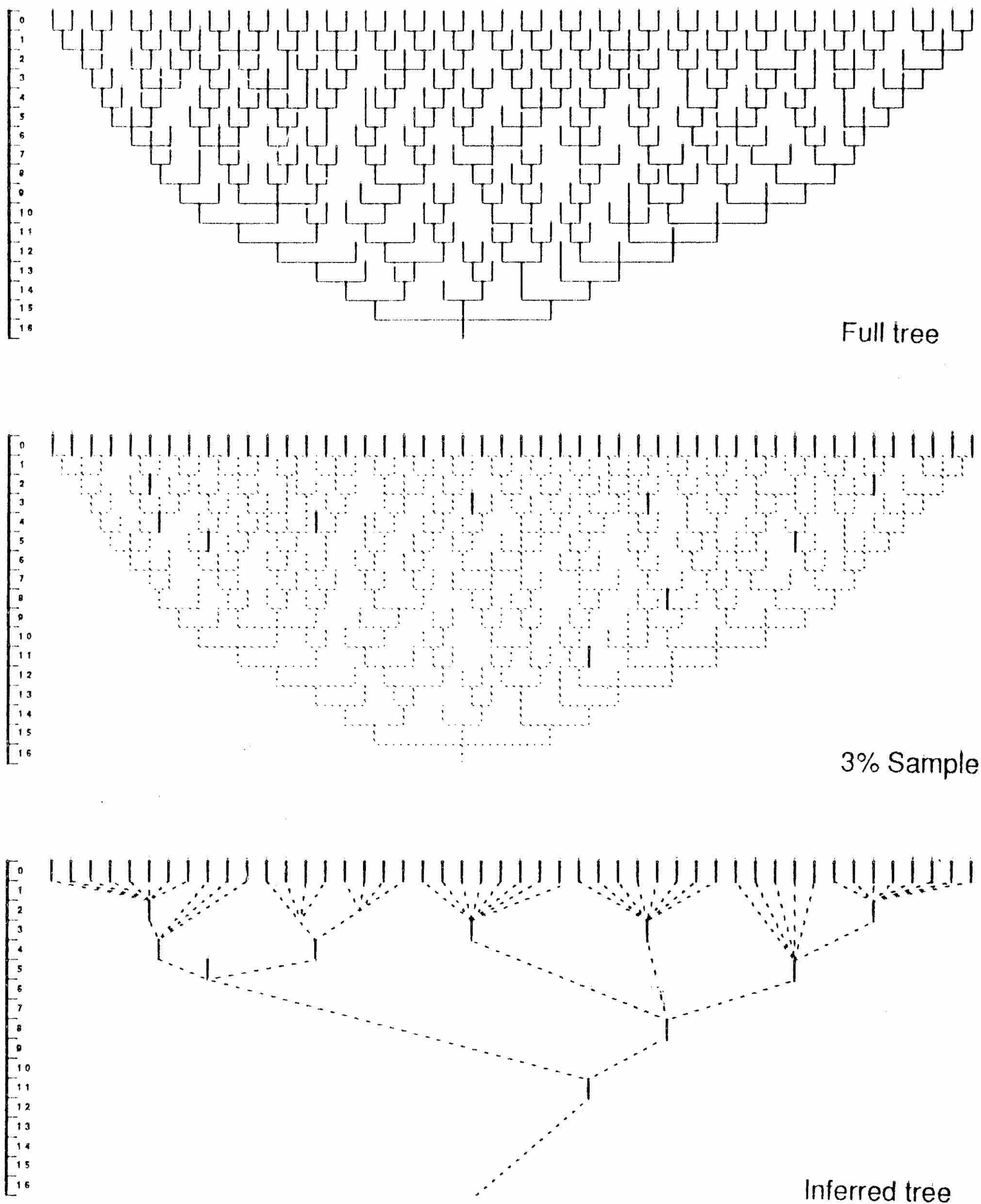


FIG. 2 Full tree: Model branching tree, with progressive expansion of number of species from 1 to 48 over a period of 16 million years. Each species has been given a standard survival time of 1 million years. 3% Sample: A typical example in which a 3% sample of fossil species ( $n=10$  species) has been randomly distributed throughout the tree. In this case, the earliest known species is dated at 11 Myr and underestimates the true time of origin of

the group by 5 million years (corresponding to a required correction factor of 45%). Inferred tree: An extreme illustration of the kind of tree that might be reconstructed if major gaps in the fossil record are not acknowledged. The time of origin of the group (based on the first known species) is likely to be seriously underestimated and fossil species may be forced into unrealistic ancestral positions.

finally to Micromomyidae (Fig. 5). The plesiadapiform families included are hence not monophyletic. Beard combined his thus expanded order Dermoptera with primates of modern aspect in the new mirorder 'Primatomorpha'. By contrast, Kay *et al.*<sup>8</sup> conclude from their cladistic analysis of craniodental features that plesiadapiforms (excluding Microsyopidae) are a monophyletic sister group of colugos and propose that all plesiadapiforms should now be transferred to the Dermoptera<sup>1,8</sup>. Their analysis indicates no connection between plesiadapiforms and primates, confirming the conclusion from a previous re-examination of evidence<sup>14</sup>.

The evidence for a specific link between plesiadapiforms and colugos is open to question. In particular, Krause<sup>15</sup> challenged the inference of gliding adaptations in *Phenacolemur* and *Ignacius* on a number of grounds. His primary criticism is that there are doubts about identification of isolated postcranial bones attributed to *Phenacolemur* and *Ignacius*, particularly the assignment of phalanges to individual digits of hand or foot. As the interpretation of isolated postcranial bones is always difficult, the inference of gliding adaptations in *Phenacolemur* and *Ignacius* is provisional until associated skeletal remains are found. More complete skeletal evidence might, for instance, show whether the atlas vertebra was butterfly shaped for the attachment of the patagium, or whether the ulna was attenuated and united at its lower end with the radius, as in modern *Cynocephalus*. Evidence from the bulla of *Ignacius*, although eliminating one of the main arguments for linking plesiadapiforms to primates, does not necessarily indicate a link with colugos (Fig. 4). Numerous mammals incorporate one or more entotympanics in the bulla and contact between the entotympanic and the basioccipital, presumably reflecting medial expansion of the bulla, could easily arise by convergence. The proposal that a lateral collar-shaped ectotympanic is a shared derived feature of plesiadapiforms and colugos<sup>3</sup> is unconvincing as the bulla of colugos is in fact formed almost entirely from the ectotympanic. In contrast to the condition in *Ignacius*, a small rostral entotympanic and an even smaller caudal entotympanic make only minor contributions to the bulla in *Cynocephalus*<sup>16</sup>. This feature is linked to a peculiarity of *Cynocephalus*: the eardrum is almost horizontal. This orientation of the eardrum was primitive for mammals and there has been a general trend towards vertical realignment<sup>14</sup>. Among modern mammals, the quasi-horizontal condition has been retained only by monotremes and certain lipotyphlan insectivores. As a retained primitive feature of *Cynocephalus*, this would suggest very early separation from all other eutherian mammals. *Cynocephalus* does show secondary reduction in the internal carotid system within the bulla, associated with increased emphasis on the vertebral arteries for supply of blood to the brain<sup>16</sup> and a similar condition can be inferred for some Paromomyidae and Plesiadapidae, although not for Micromomyidae<sup>2,11</sup>. But such ontogenetic suppression of a pre-existing system could easily have arisen convergently.

Several other points are pertinent. First, the Palaeocene/Eocene Plagiomenidae have long been regarded as fossil relatives of colugos because of dental resemblances<sup>17</sup>. But new basicranial evidence revealed that *Plagiomena* greatly differs from *Cynocephalus*, indicating that the dental similarity is convergent<sup>18</sup>. This provides yet another example of the danger of basing inferred relationships exclusively on dental evidence. More recently, *Dermotherium* from the late Eocene of Thailand has been identified as a direct relative of modern colugos<sup>19</sup>.

Although the evidence is restricted to a lower jaw fragment containing only two molars, the resemblance to *Cynocephalus* is impressive and may well indicate that the colugos existed as a distinct lineage at least by the late Eocene. *Dermotherium* seems to rule out the Plagiomenidae<sup>17</sup> or the early Eocene Placentidentidae of Europe<sup>20</sup> as relatives of *Cynocephalus*.

Curiously, little has been said about possible dental evidence linking plesiadapiforms to colugos. For example, the cladistic

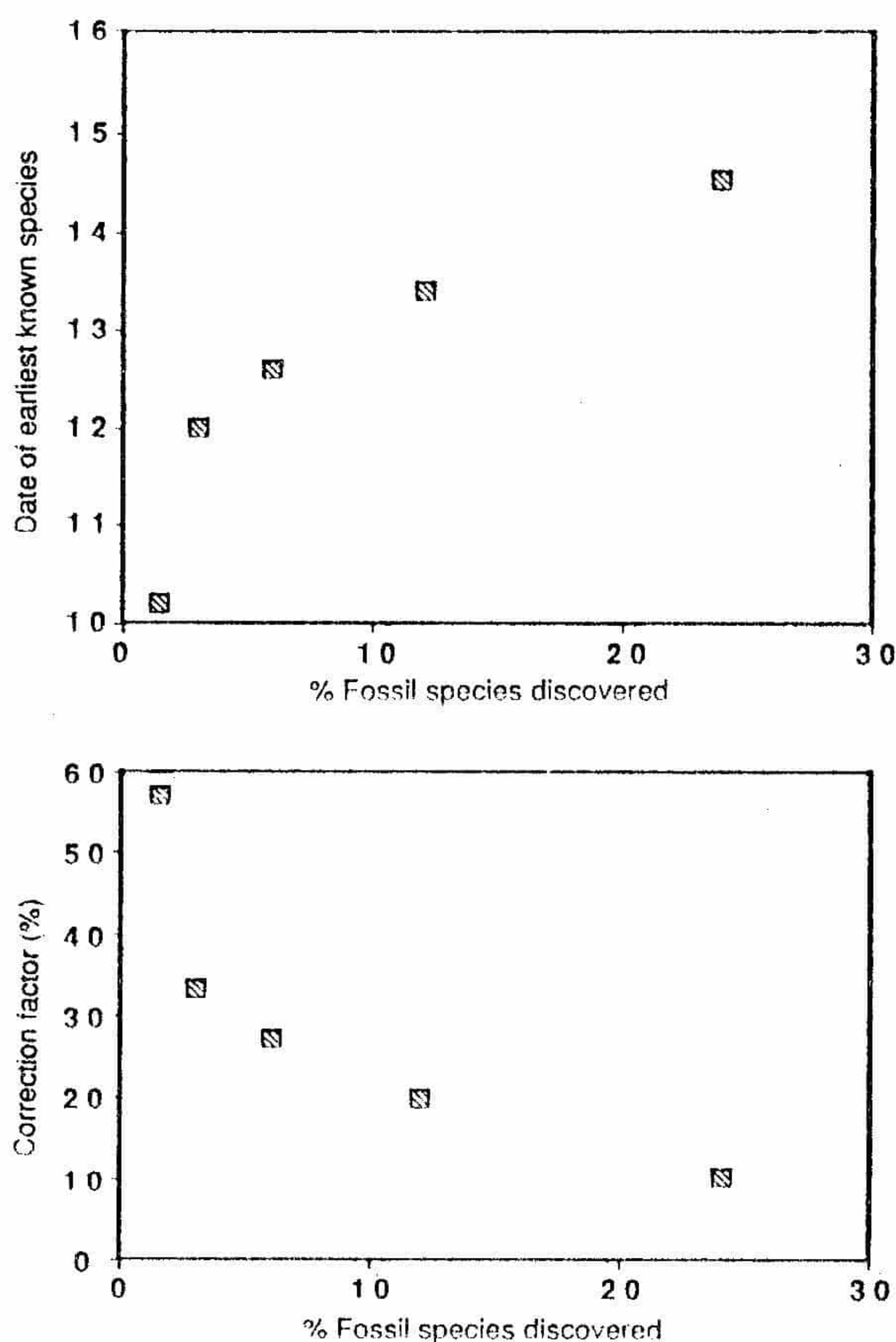
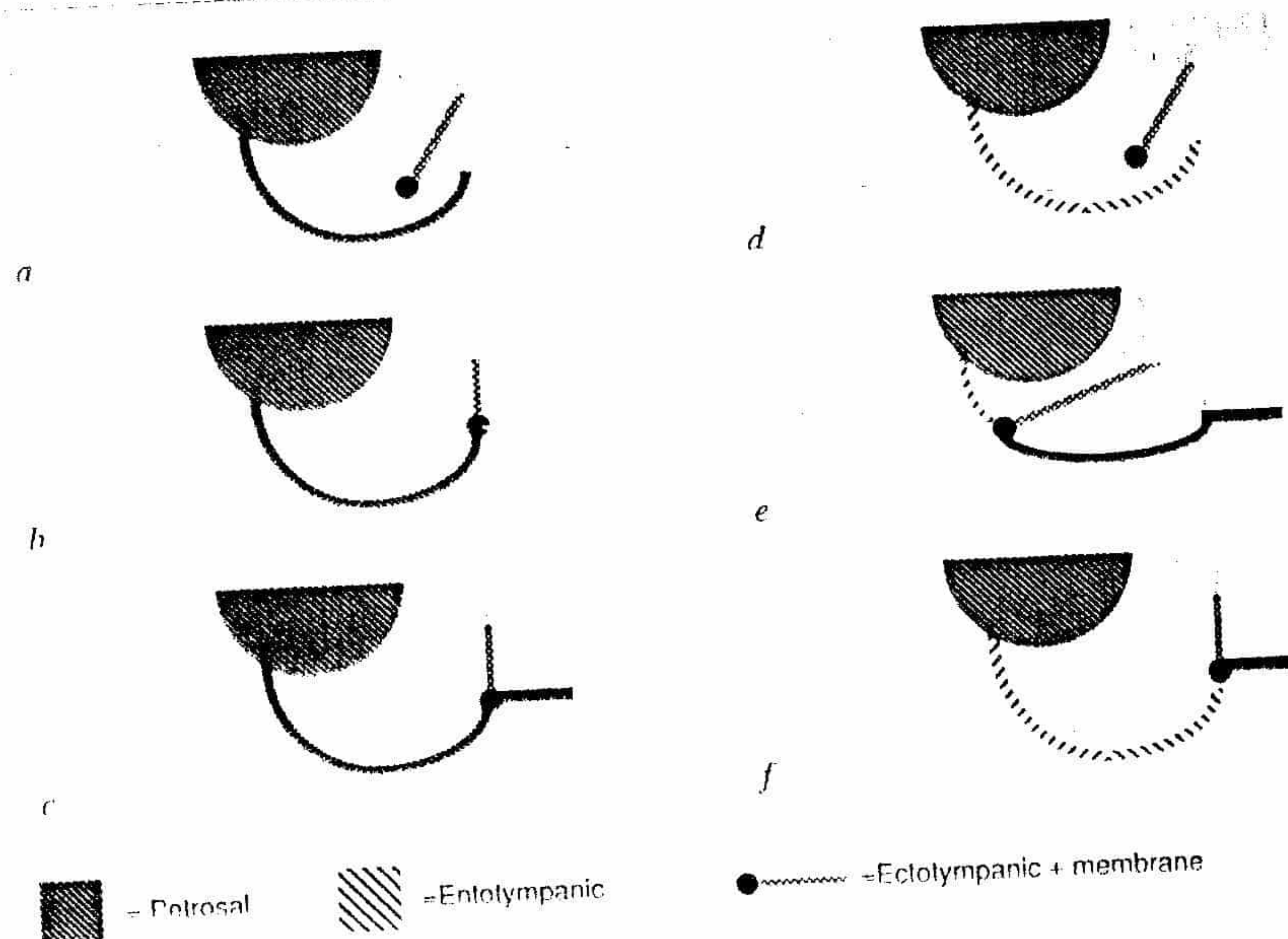


FIG. 3 Upper curve: Plots of average values obtained from 25 simple simulations of various sampling densities in the fossil record (1.5%, 3%, 6%, 12%, 24%), taking the tree in Fig. 2. Relative to a true origin at 16 Myr ago, the date of the earliest known species is close to 10 Myr at a sampling level of 1.5% and is below 15 Myr even with a sampling level of 24%. Lower curve: Correction factors (% value to be added) for such simple trees can be calculated for inferring the actual time of origin from the date of the first known fossil species at different sampling densities of the fossil record.

analysis of Kay *et al.* included no dental evidence<sup>8</sup>. Supposed resemblances in the molar teeth between plesiadapiforms and primates of modern aspect provided the main basis for inferring a phylogenetic link, although this evidence has been questioned<sup>14</sup>. Surely, if plesiadapiforms are linked to colugos instead of primates, we should expect plesiadapiforms to show some dental resemblance to *Cynocephalus*. Modern colugos in fact have a highly unusual dentition, with comb-like crowns on the procumbent lower incisors and serrated upper incisors and upper and lower canines. The upper molar teeth are essentially triangular and bear three main cusps, presumably a primitive feature, and all the cheek teeth possess tall, sharp cusps adapted for shearing. *Cynocephalus* reportedly feeds primarily on leaves, but the dietary function of the comb-like lower incisors has yet to be explained. Comparison between *Cynocephalus* and Paromomyidae merely shows that they are dentally very different<sup>19</sup>. It is, of course, possible that the dental features of *Cynocephalus* have become so specialized that its relationships are no longer evident<sup>6</sup>. For instance, Beard proposes a *Nannopithecus*-fold on the upper molars as a shared derived feature characterizing the 'Primatomorpha' and then infers that it disappeared without trace from colugos through evolutionary reversal<sup>13</sup>. This dental feature is, in fact, lacking from the earliest known fossil primates of modern aspect, so it is more likely to have arisen by convergence even within primates<sup>8,14</sup>. In sum, plesiadapiforms, formerly 'dental primates', are no more than 'postcranial colugos'.

FIG. 4 Schematic transverse sections of the auditory bulla in primates (left) and non-primates (right). In each case, the skull midline is on the left and the outer skull margin is on the right. In all living primates, the bulla wall is formed from the petrosal, but the relationship between the ectotympanic ring and the bulla varies between groups: enclosed in lemurs (a); fused to the outer margin in the lorises group and in New World monkeys (b); fused to the outer margin and extended to form a tube in tarsiers and Old World simians (c). In tree shrews (d), the bulla wall is formed from an entotympanic and the ectotympanic ring is enclosed. In colugos (e), the bulla wall is formed mainly from the ectotympanic, with a small entotympanic contribution. Note the almost horizontal orientation of the tympanic membrane (eardrum). In the plesiadapiform *Ignacius* (f), the bulla wall is formed mainly from an entotympanic, with the ectotympanic fused to the outer margin and extended to form a tube. There is convergence in general form (but not in constitution) between tree-shrews and lemurs (d versus a) and between plesiadapiforms and tarsiers/Old World simians (f versus c).



If colugos and plesiadapiforms together constitute the sister group of primates, all should possess shared derived features. Beard's cladistic analysis<sup>13</sup>, based mainly on postcranial traits, seems to demonstrate the existence of a special set of adaptations for vertical postures and climbing<sup>6</sup>. By contrast, the analysis of cranial features by Kay *et al.*<sup>8</sup> leads to the incompatible conclusion that primates are linked not to plesiadapiforms and colugos but to tree-shrews and bats. Moreover, in addition to the horizontal orientation of its eardrum (Fig. 4), *Cynocephalus* shows several features ignored in both analyses that would be highly unusual in any direct relative of primates. The brain, for instance, is remarkably small, with dominant olfactory components and diminutive cerebral hemispheres (Fig. 6). Unfortunately, a report on relative brain size in *Cynocephalus*<sup>21</sup> cited an immature body weight of only 810 g. Taking a revised adult body weight of 1.4 kg and a cranial capacity of 6.9 ml, the index of cranial capacity (ICC)<sup>14</sup> is only 1.5, on the boundary between 'basal' and 'advanced' insectivores. This value is well below the lower limit for modern primates (2.4) and is instead close to the value of 1.4 for the Eocene primate *Adapis*, which lived some 40 million years ago (Fig. 6). As a further strikingly primitive feature, although *Cynocephalus* has only a single neonate, it is apparently extremely poorly developed (altricial) and has been described as 'marsupial-like'<sup>22</sup>. Modern primates are uniformly characterized by neonates with well defined precocial features<sup>13</sup>.

Inference of a link between primates, plesiadapiforms and colugos is connected with a recent revival of the concept of the superorder Archonta, originally grouping primates, colugos, bats, tree-shrews and elephant-shrews<sup>23</sup>. Although the terrestrial elephant-shrews are now generally excluded, there have been repeated proposals of relationships among some or all of the remaining forms, which typically have some connection with arboreal habits. Proposed inclusion of tree-shrews in the order Primates has a long history, but there is no convincing evidence of shared derived features and it is preferable to allocate them to their own order Scandentia<sup>14,24</sup>. MacKenna's proposal<sup>25</sup> that bats, colugos, tree-shrews and primates together form a phylogenetic unit was later supported on the basis of postcranial evidence<sup>26</sup>, although the status of the bats remained uncertain, whereas immunological evidence apparently linked colugos, tree-shrews and primates to the exclusion of bats<sup>27</sup>. On morphological grounds, Shoshani identified a phylogenetic association between bats, colugos, tree-shrews and primates<sup>28</sup> and Novacek cited limited support for a concept of Archonta in which tree-shrews are allied with primates and colugos with bats<sup>29,31</sup>. By

contrast, an analysis of amino-acid sequences in a tandem alignment of up to seven proteins<sup>32,33</sup> linked bats and tree-shrews with insectivores and carnivores and associated primates with lagomorphs and rodents.

In a new variation on the archontan theme, Pettigrew<sup>34</sup> reported evidence from the visual system (pattern of retinotectal projection) indicating that the fruit-bats (Megachiroptera), but not other bats (Microchiroptera), are directly related to primates. Following a cladistic analysis of 24 neural characters, this proposal was then expanded into the 'flying primate hypothesis' linking primates, fruit-bats, colugos and tree-shrews (in that order)<sup>35</sup>, with paromomyids being included as purported relatives of colugos in due course<sup>36</sup>. This hypothesis has been opposed because it conflicts with extensive morphological evidence indicating a monophyletic origin for bats<sup>31,37,38</sup>. It has also emerged that the pattern of retinotectal projection in the fruit-bat *Rousettus aegyptiacus* is not primate-like but follows the general mammalian scheme<sup>39</sup>, suggesting that a primate-like pattern may have evolved convergently in some fruit-bats (such as *Pteropus*). Further, a sequence analysis of  $\epsilon$ -globin genes for 17 mammal species<sup>40</sup> produced very convincing evidence for a monophyletic origin of bats and linked tree-shrews to lagomorphs rather than to primates. Monophyly of bats was independently confirmed by an analysis of the mitochondrial cytochrome oxidase subunit II gene<sup>41</sup>. This analysis also groups *Tupaia* and *Cynocephalus* (but not bats) with primates, apparently providing support for a curtailed archontan assemblage. In fact, *Cynocephalus* consistently emerged as closer to primates than *Tupaia*. As the comparisons include only nine placental mammal species, however, these results must be regarded as tentative.

Overall, the superordinal relationships of primates remain unclear. Even authors who accept the existence of a group 'Archonta' generally do not agree on its composition or internal arrangement and no consistent picture is provided by molecular comparisons<sup>42</sup>. All such interpretations are based on undoubted morphological similarities between bats, colugos, tree-shrews and primates, but their interpretation is questionable. Most authors assume that the ancestral placental mammals were terrestrial and accordingly interpret any arboreal adaptations of 'archontans' as shared derived features indicating a specific common ancestry. If, however, the ancestral placental mammals were at least partially arboreal in habits, the similarities shared by colugos, bats, tree-shrews and primates can be interpreted as a mixture of primitive retentions and convergent adaptations<sup>14</sup>. In this respect, an important new development has been

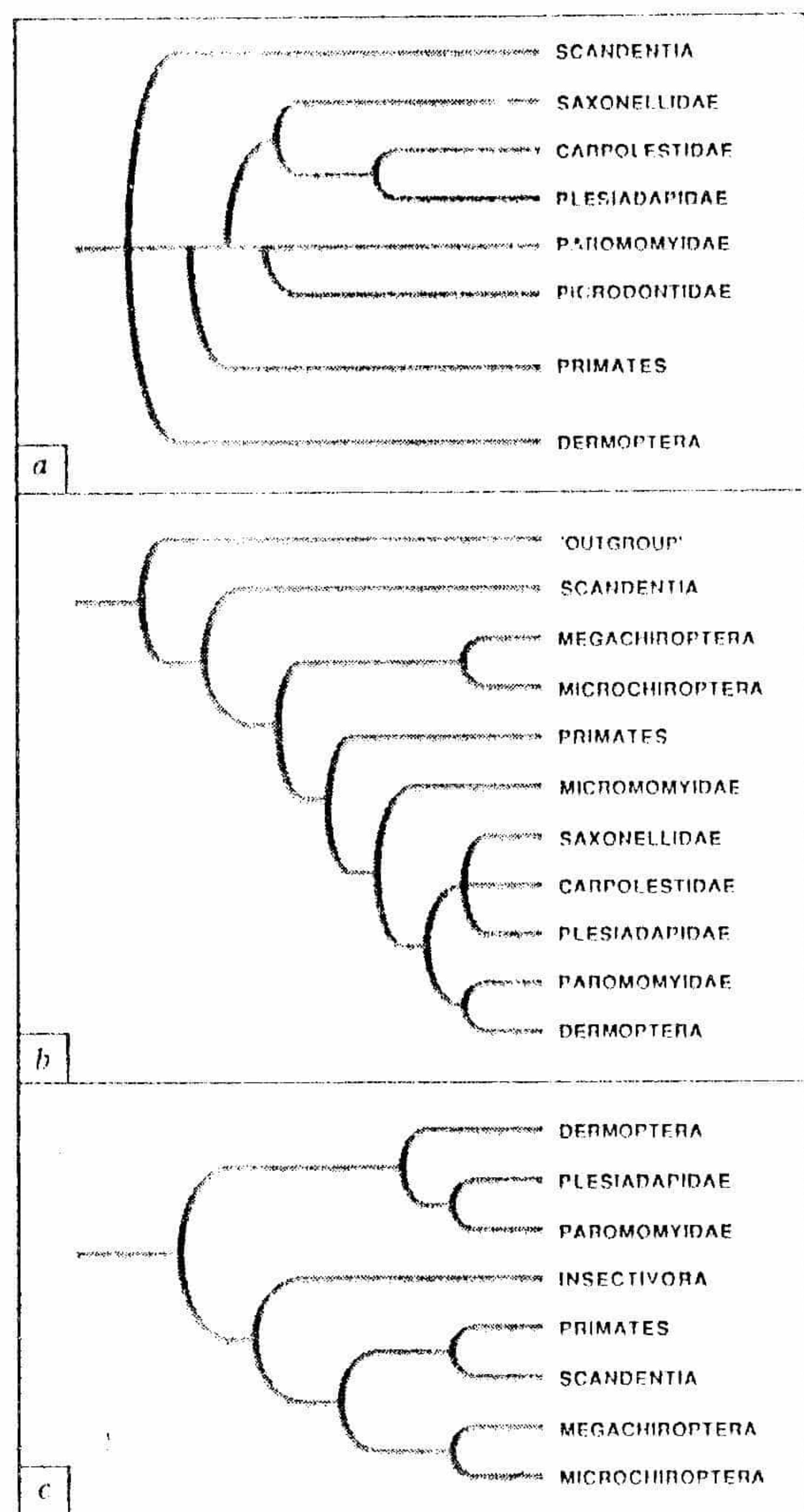


FIG. 5 Alternative interpretations of the relationships between dermopterans, plesiadapiforms and primates, following: a, Szalay and Delson<sup>1</sup>; b, Beard<sup>13</sup>; and c, Kay *et al.*<sup>8</sup>.

the description of the postcranial skeleton of the Jurassic eupantothere *Henkelotherium*<sup>43</sup>, which is surprisingly advanced and shows several adaptations for arboreal life. Therian mammals (marsupials and placentals) are probably derived from a eupantothere stock, so this new evidence strengthens the inference that marsupials and placentals both had an arboreal origin.

### Affinities of the Adapidae

New discoveries of fossil adapids ('lemuroids') have included important finds both in North America and in Europe. In North America, where all or most forms can be allocated to the subfamily Notharctinae, the main advance has been a significant increase in our knowledge of the early genera *Cantius* and *Pelycodus*. The later forms, *Notharctus* and *Smilodectes*, have long been documented by some of the best material available for fossil primates<sup>1,44-46</sup>, but the earlier North American adapids were known essentially from isolated teeth and jaw fragments. Indeed, well preserved skulls of these earlier representatives have yet to be discovered. A study of more than 100 new foot elements from 7 species of *Cantius* and (?) *Pelycodus*<sup>47</sup> has now partly improved our knowledge. Not surprisingly, *Notharctus* and *Smilodectes* are apparently derived in comparison with *Cantius*, although only in subtle details. Overall, these new finds fit expectation quite closely. It is interesting, however, that the tarsal bones changed relatively little during the early radiation of *Cantius* and (?) *Pelycodus*, although the dentition changed

quite markedly over the 5-million-year period concerned. This is a particularly clear example of mosaic evolution. Comparison of foot bones of *Cantius*, *Notharctus* and *Smilodectes* with those of modern lemurs and lorises provides little evidence of a specific link between the Eocene forms and modern strepsirrhine primates. The only features that may indicate a specific link between all adapids and modern strepsirrhines are morphological features of the ankle region (sloping talo-fibular facet; lateral groove for the flexor hallucis longus; ventral extension of the navicular facet for the cuboid). Such features have been cited<sup>48</sup> in support of the interpretation that the adapids are the sister group of modern lemurs and lorises, and this inferred link has been reinforced with the suggestion that adapids and strepsirrhines show shared derived features of the hand and wrist associated with an emphasis on hand postures involving ulnar deviation<sup>49</sup>. A link between adapids and modern strepsirrhines has also been proposed on the basis of resemblances in the incisor-canine complex<sup>50</sup>. Taken together, these various lines of evidence provide suggestive but by no means conclusive indicators of a connection between adapids and strepsirrhines.

The main surprises with respect to the adaptive radiation of the adapids have come from recent studies of European forms. The best-known genera with respect to craniodental remains continue to be *Adapis* and *Leptadapis*, still mainly represented by numerous well preserved skulls discovered long ago in late Eocene deposits of France. Although several species were originally identified<sup>51</sup>, most recent authors have recognized just the two species *Adapis parisiensis* and *Leptadapis magnus*. A comprehensive re-examination of these skulls has now convincingly shown that quantitative variation among the skulls attributed to either species greatly exceeds that found within any modern primate species, even exceeding the level of variation across closely related genera for some features<sup>52,53</sup>. Excessive variation in dental dimensions of specimens allocated to '*Adapis parisiensis*' had already been noted by Gingerich<sup>54,55</sup> and it now seems highly likely that this taxon and '*Leptadapis magnus*' in fact group a number of species together<sup>56</sup>. An earlier suggestion<sup>57,58</sup> that quantitative differences among skulls of *Adapis* or *Leptadapis* reflect sexual dimorphism must now be re-examined. The new findings do not necessarily show that sexual dimorphism was lacking in *Adapis* and *Leptadapis*, but such sexual differences must now be sought within the individual species identifiable on the basis of Lanèque's analyses. For the

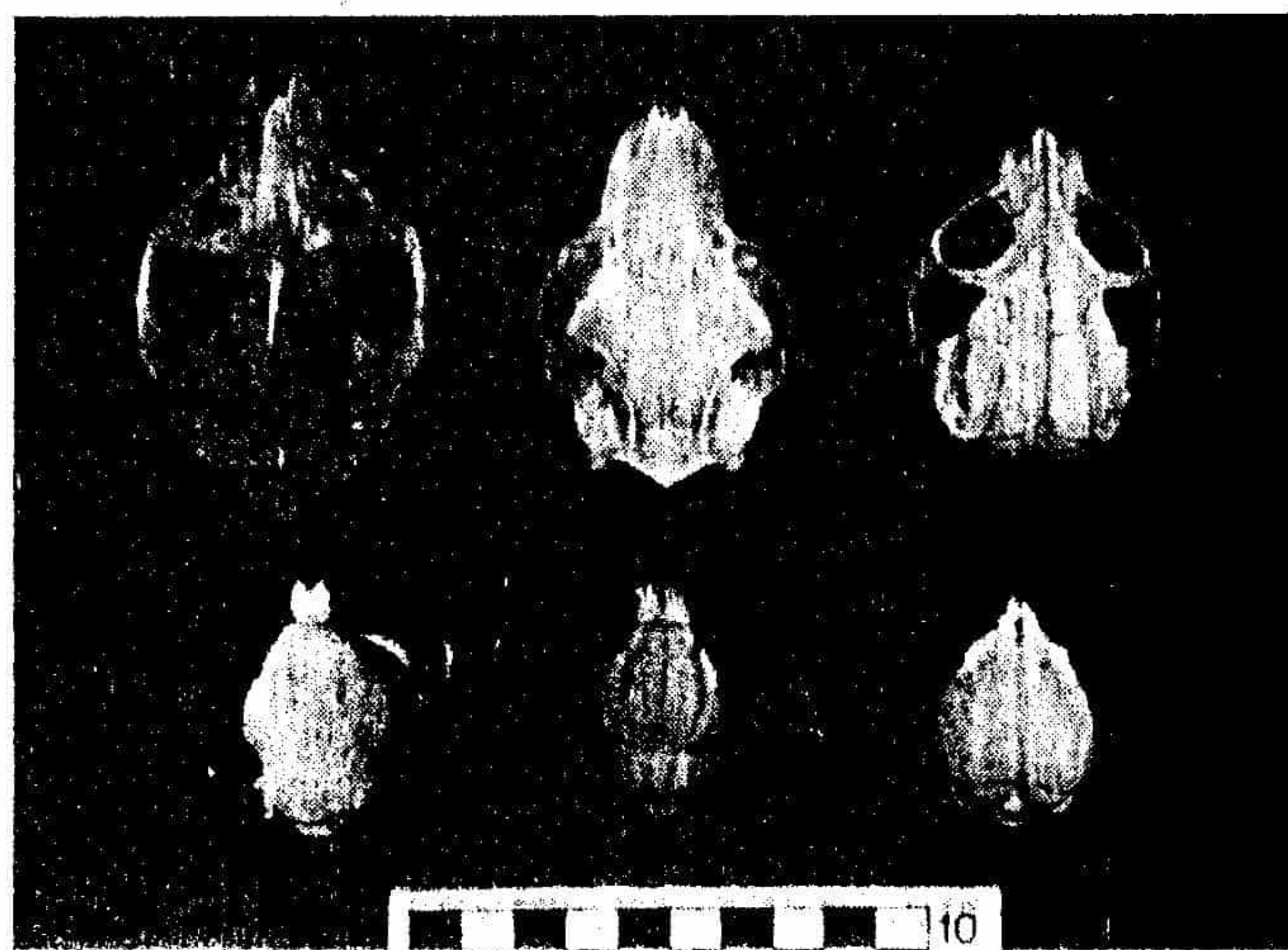


FIG. 6 Skulls and endocasts (casts of the brain cavity) of *Adapis parisiensis* (left), *Cynocephalus variegatus* (centre) and *Perodicticus potto* (right). In both the Eocene *Adapis* and the modern *Cynocephalus* the endocast is very small relative to body size and the neocortex is diminutive, as is indicated by the dorsal exposure of the olfactory bulbs and the cerebellum. Note also the laterally facing orbits, the lack of a postorbital bar and the wide separation of the orbits in *Cynocephalus*, contrasting starkly with the typical primate pattern in *Adapis* and *Perodicticus*.

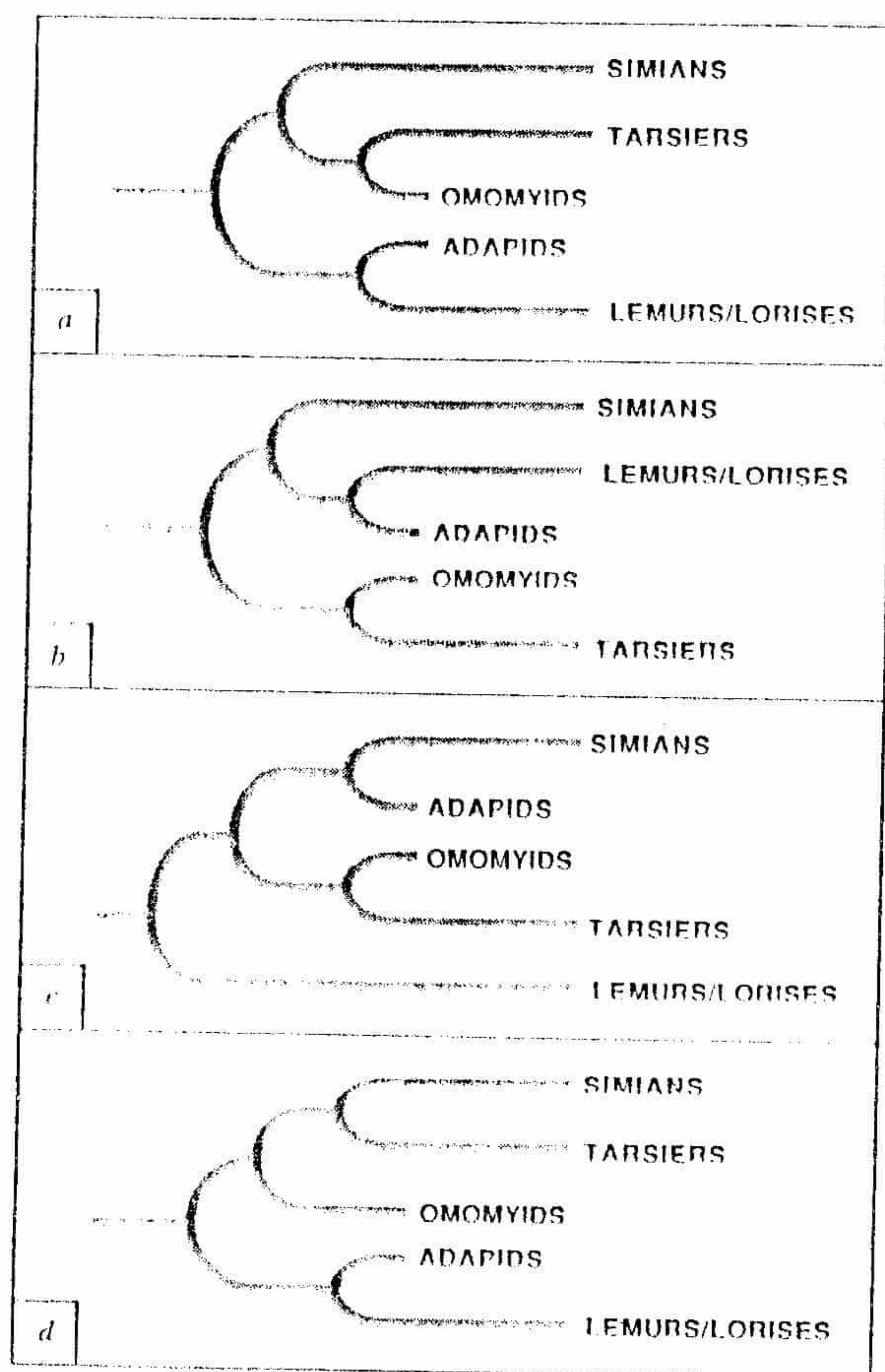


FIG. 7 Four alternative interpretations of the relationships between adapids, omomyids and living primates. *a*, The omomyophile hypothesis<sup>78</sup>, with simians deriving from an omomyid-like stock; *b*, one version of the adapid hypothesis (the lemurphile hypothesis<sup>78</sup>), with both simians and strepsirrhine primates originating from an adapid-like stock; *c*, a second version of the adapid hypothesis (the lemurphobe hypothesis), with simians originating from an adapid-like stock, whereas strepsirrhine primates had a distinct origin; *d*, the tarsiphile hypothesis<sup>78</sup>, with simians deriving from a tarsier-like ancestor.

time being, the only remaining evidence for sexual dimorphism in Eocene primates is that reported for the upper canine teeth of *Notharctus ventricolus*<sup>59</sup>. In that case, the specimens concerned came from the same stratigraphic horizon and showed two different canine sizes despite the fact the molar teeth were all very similar in size and shape, so it is less likely that interspecific differences were confused with differences between the sexes.

In contrast to information on the North American representatives, our understanding of European adapids has long been severely constrained by the lack of associated postcranial remains. Isolated postcranial bones have been attributed to *Adapis* and *Leptadapis* on the grounds of size and primate-like features, but calcanei (heel-bones) attributed to these two genera lack the relative elongation of the anterior segment that is otherwise universally found among fossil and living prosimian primates<sup>14,60,61</sup>. It is possible, as concluded from the detailed study conducted by Dagosto<sup>62</sup>, that *Adapis* and *Leptadapis* exhibited extensive secondary specialization of the postcranial skeleton, accounting for departures from the typical primate pattern. Additional evidence of the puzzling nature of postcranial elements attributed to *Adapis* and *Leptadapis* is provided by a recent study<sup>63</sup> in which body weight of fossil primates was estimated from dimensions of the tarsal bones. Overall, there is relatively good agreement between these postcranial estimates and those derived from skulls and/or teeth. There is one surprise

in that *Adapis* skull measurements consistently indicate a body weight of at least 2 kg (ref. 14), whereas postcranial elements attributed to this genus indicate a body weight of only 1 kg; for *Leptadapis*, both skulls and postcranial elements indicate the same body weight of about 8.5 kg. It is possible that this disparity will disappear when the different species currently subsumed in '*Adapis parisiensis*' have been clearly separated, but only the discovery of associated cranial and postcranial remains would settle the issue clearly.

In recent years, postcranial remains of a number of other European adapids have been reported. Most finds have come from the Messel deposits of southern Germany, which have yielded five specimens<sup>64-68</sup>. Unfortunately, the specimens are all incomplete and three of them cannot be identified even to genus level, because the skull and teeth have not been preserved, and they have hence been recognized simply as adapids of some kind. One specimen, however, consists of the anterior part of the body including a crushed skull and has been identified as *Europolemur koenigswaldi*, while a second specimen has been identified as the rear end of the same species. These specimens indicate that *Europolemur* was a relatively small-bodied arboreal climber and leaper with extremities adapted for grasping<sup>66</sup>. Another crucial new specimen from a different site is the crushed skull and skeleton of *Pronycticebus neglectus* from the Geiseltal deposits of eastern Germany<sup>69</sup>. The genus *Pronycticebus* was previously documented only by a single skull from France and study of the German skeleton indicates that this primate, which probably had a body weight close to 750 g, was an arboreal climber and leaper with an insectivorous/frugivorous diet. Finally, recent excavations in northern Spain have yielded more than 500 specimens representing most of the postcranial skeleton attributed to the hitherto poorly known genus *Anchomomys*<sup>70</sup>. This genus is of particular significance because its body size (about 120 g) is much smaller than that of other adapids. Interestingly, the postcranial elements of all of these new adapid finds are closely similar to those of the North American notharctines and unlike those attributed to *Adapis* and *Leptadapis*.

One possible interpretation of the new finds is that at least some postcranial elements attributed to *Adapis* and *Leptadapis* do not in fact belong to those genera. By contrast, if the allocations are correct, it follows that *Adapis* and *Leptadapis* are quite distinct from most other known adapids. Gingerich<sup>71</sup> originally distinguished between an '*Adapis* group' and a '*Protoadapis* group' in Europe, although he did not identify a major separation between them. Later, citing dental characteristics and postcranial features, Franzen<sup>66</sup> proposed that the European adapids should be split into two distinct groups: (1) *Adapis*, *Leptadapis*, *Microadapis* and (?) *Caenopithecus*; (2) *Cantius*, *Protoadapis* and *Europolemur*. The second group, characterized (for example) by lower-crowned molars with weakly defined crests, by a transverse oblong shape of the upper molars and by more limited molarization of the premolars, roughly corresponds to the tribe Protoadapini recognized by Szalay and Delson<sup>1</sup>. This tribe also includes *Pronycticebus* and the distinctive North American genus *Mahgarita*. Although the Protoadapini are morphologically closer to the North American forms and are represented in Europe throughout the Eocene, *Adapis*, *Leptadapis*, *Microadapis* and *Caenopithecus* appear abruptly towards the end of the middle Eocene<sup>72</sup>. For now, it is probably best to regard the *Adapis* group as an aberrant sideline that may or may not be a part of a monophyletic radiation of adapids. By contrast, the main group is of particular interest because of suggestions that the origins of simians may be traced specifically to the Protoadapini (Box 2).

It is also significant that a single lower molar tooth ( $M_2$ ) from a presumed middle Eocene locality in South-East Asia has been identified as an adapid<sup>73</sup>. Confirmation of this identification would greatly expand the known geographical range of Eocene adapids and could lead to new interpretations of early primate evolution.

BOX 2 What was the origin of the simian primates?

Four main hypotheses have been proposed to explain simian origins: (1) the tarsier hypothesis, deriving simians from a tarsier-like ancestor<sup>106</sup>; (2) the omomyid hypothesis, deriving simians from an omomyid stock<sup>107</sup>; (3) the adapid hypothesis, deriving simians from an adapid stock<sup>108</sup>; (4) the pre-simian hypothesis, deriving simians from hypothetical ancestors in Africa during the early Tertiary<sup>109</sup> or in Gondwanaland during the upper Cretaceous<sup>110</sup>. A widely favoured interpretation has been that omomyids gave rise to both tarsiers and simians (Fig. 6a). That interpretation has been increasingly challenged, however, and several authors now prefer some form of the adapid hypothesis instead. One version is that adapids gave rise to both simians and strepsirrhine primates (Fig. 6b)<sup>48,71,79</sup>, but this is in direct conflict with abundant evidence from living forms that tarsiers and simians form a monophyletic group. An alternative version is that adapids exclusively gave rise to simians (Fig. 6c)<sup>81,96,111-114</sup>. Another possible interpretation<sup>78</sup>, according to which the omomyids branched away before the separation between tarsiers and simians (Fig. 6d), in effect amounts to a revival of the tarsier hypothesis.

With respect to the known fossil record, the discussion boils down to the question whether omomyids or adapids are most likely to have given rise to simians. There is little if any direct evidence for a link between omomyids and simians (Fig. 6a or d); instead there has generally been an indirect chain of argument that tarsiers are related to omomyids, that tarsiers are also related to simians and that omomyids must thus be related to simians. If tarsiers are not, in fact, related to omomyids, the argument for an omomyid origin of simians virtually collapses.

The alternative proposal that simians are derived from adapids has been backed on the basis of a seemingly impressive list of similarities, including increased body size, vertically implanted spatulate incisors, large interlocking canines with a honing relationship between the upper canine and the anterior lower premolar, sexual dimorphism in body size and canine size, a quadratic form of the molars, fusion of the anterior junction (symphysis) between the two halves of the lower jaw, an annular form of the ectotympanic, unfused tibia and fibula and lack of elongation of the calcaneum and navicular<sup>40,79,111</sup>. Some of these characters can be discounted because they are likely to be primitive for primates generally (for example, large canines; annular ectotympanic; unfused tibia and fibula; non-elongated calcaneum and navicular), whereas others have developed so often during mammalian evolution that they carry little weight (for example, increased body size; quadratic molars). Further, the evidence for sexual dimorphism in adapids now needs careful re-examination and such dimorphism is in any case neither unique to nor ubiquitously present in simian primates.

Spatulate incisors and fusion of the lower jaw symphysis have all arisen repeatedly in the evolution of primates and other mammals. Indeed, within the primates these features were developed independently in various

large-bodied subfossil lemurs and similarities in jaws and teeth between *Archaeolemur* and Old World monkeys provide one of the most striking cases of convergent evolution known for primates. Further, fusion of the lower jaw is not found in all adapids. It was lacking in the earliest adapids (*Cantius*; *Pelycodus*) and was absent even in some later forms, such as *Smilodectes*<sup>115,116</sup> and *Pronycticebus*<sup>69</sup>, so this feature must have arisen several times independently within the Adapidae<sup>14,48,66</sup>. Symphyseal fusion occurred late in development in *Notharctus*; only in *Adapis*, *Leptadapis* and (presumably) *Mahgarita* did fusion occur early in life as in simians. Hence, if simians are to be derived from adapids on grounds of symphyseal fusion, they must presumably be derived from one of these genera. First, however, *Adapis*, *Leptadapis* and *Mahgarita* are all late Eocene forms, most probably too recent for simian ancestry. Second, it now seems that in the earliest yet known simians, such as late Eocene *Catopithecus*<sup>96</sup> and *Arsinoea*<sup>97</sup>, the symphysis may not have been fused, in which case symphyseal fusion must have developed after the origin of these simian primates.

Rasmussen and Simons<sup>113</sup> narrowed the possible source of simians among adapids to the tribe Protadapini, and Rasmussen<sup>114</sup> subsequently noted additional specific resemblances between the North American genus *Mahgarita* and simians. These included: large promontory canal; stapedia canal reduced or absent; pneumatized petromastoid region; lateral transverse intrabullar septum; probably no free ectotympanic ring; mandible firmly fused and robust; mandibular symphysis with a transverse torus; short, deep maxilla; detailed similarities in occlusal features of upper molars and other teeth. Although these similarities are intriguing, they can only be of phylogenetic significance if simians are derived directly from *Mahgarita* or some similar ancestral form. One must bear in mind the possibility that sharing of a number of similarities between certain adapids and simians may be attributable to convergence.

Derivation of simians from either adapids or omomyids remains problematic because the known fossil skulls uniformly lack any indication of postorbital closure by a bony partition and the frontal bones remain unfused into adult life. Similarly, known adapid skulls show no sign of the early marked increase in relative brain size that distinguishes simians from prosimians overall and is already established in *Aegyptopithecus*, although such an increase is in fact identifiable in Eocene omomyids<sup>14,48</sup>. Finally, no known fossil skulls before the Fayum simians show the loss of the median gap between the upper incisors that characterizes tarsiers and simians and would indicate loss of the rhinarium (haplorhine condition). In short, even if simians can be derived from adapids or omomyids, vital transitional evidence is still lacking. In other words, the pre-simian hypothesis, tracing simians to an as yet undocumented ancestral stock in the southern continents, is still a viable option.

## Affinities of the Omomyidae

The status of the early Tertiary Omomyidae ('tarsioids') is arguably the most controversial issue concerning the evolutionary tree of primates and seems set to remain so for the foreseeable future. Not long ago, it was widely accepted that omomyids are directly linked to the ancestry of tarsiers. Similarities between tarsiers and at least some omomyids exist in the bell-shaped upper dental arcade, unusual foreshortening of the lower jaw associated with a reduction in number of teeth relative to the upper jaw, a tubular meatus in the bulla and adaptation of the postcranial skeleton for leaping. In addition, omomyids do seem to resemble both tarsiers and simians in possessing a short facial skull associated with a relatively small nasal fossa<sup>74</sup>, and there is some evidence of limited reduction in the size of the olfactory bulbs<sup>14</sup>. Although it was suggested that omomyids resemble tarsiers and simians in possessing an enlarged promontory artery that enters the bulla posteromedially<sup>75</sup>, *Necrolemur* apparently possessed a relatively large stapedia artery and the medial entry into the bulla may in fact be primitive for mammals<sup>76,78</sup>. Rosenberger<sup>74</sup> has noted further similarities in the basicranium between some omomyids and tarsiers, including a flexed basi-cranial axis, encroachment of the bulla on the pterygoid fossa associated with extensive laminar confluence between pterygoid and bulla, and a deeply guttered, slot-like shape of the glenoid fossa. But there has always been an undercurrent of doubt about

the inference of a link between omomyids and tarsiers and interpretation of the fossil record is hampered by the fact that modern tarsiers have molar teeth that seem extremely primitive. The upper molars have a simple three-cusped pattern, and the paraconid cusp (commonly lost in fossil and living primates of modern aspect) is still present in the lower molars. Further, while it is true that omomyids resemble tarsiers in possessing paraconids on their lower molars, this is no more than retention of a primitive feature. Hence, it is difficult to link omomyids to either tarsiers or simians through dental morphology.

One alternative view is that the omomyids are, indeed, related to tarsiers and that both are appropriately allocated to the infraorder Tarsiiformes, but that the latter has no connection with simians. An extreme version of this interpretation was advocated by Gingerich<sup>11</sup>, who allied Tarsiiformes with Plesiadapiformes in the suborder Plesitarsiiformes because of apparent similarities in the structure of the bulla and in the anterior lower dentition. All other primates of modern aspect (lemurs, lorises and simians) were combined in a second suborder Simiolemuriformes. This arrangement, however, requires convergent evolution of many features present in all living and fossil primates of modern aspect (including tarsiiforms) but lacking in plesiadapiforms. Gingerich subsequently accepted a model of primate evolution incorporating three adaptive grades: Plesiadapiformes, Prosimii (including lemurs, lorises, tarsiers,

Adapidae and Omomyidae) and Anthropoidea<sup>12</sup> and later retracted his suggestion of a link between plesiadapiforms and tarsiforms<sup>79</sup>. His revised model, however, incorporated no direct connection between tarsiforms and simians. This left the way open for the less extreme proposal that the origin of simians within the prosimian grade is to be traced not to omomyids but to adapids (Box 2). In fact, both of these alternative proposals are in direct conflict with many similarities, several of which are unique, linking modern tarsiers to simians<sup>14,80</sup>. It is, of course, conceivable that some similarities have arisen convergently. For instance, developmental evidence seems to indicate that the almost complete bony eye-socket of tarsiers and simians (a feature found in no other mammals) may have arisen independently<sup>81</sup>. Nevertheless the sheer numbers of apparent derived features in independent systems shared by tarsiers and simians render convergence in all of them extremely unlikely.

A different challenge to the consensus view linking omomyids, tarsiers and simians comes from the view that there is no specific link between omomyids and tarsiers<sup>77,82</sup>. One feature linking modern tarsiers and simians (haplorhine primates) is the complete loss of the rhinarium (an area of naked skin surrounding the nostrils). This derived feature, which is highly unusual among mammals, is correlated with closure of a median gap between the upper incisors that occurs in association with the rhinarium in lemurs and lorises (strepsirhine primates). It is now known that the European omomyids *Necrolemur* and *Pseudoloris* still had a gap between the upper incisors<sup>77,80</sup>. It is therefore possible that a rhinarium was still present in omomyids, although its loss could have preceded closure of the gap between the incisors. In any event, broad reviews of the evidence<sup>77,78,80,83</sup> have indicated fairly clearly that the relationship between tarsiers and simians is probably closer than that between tarsiers and omomyids. Indeed, Schmid<sup>82</sup> has suggested that omomyids should be classified together with lemurs, lorises and adapids in the suborder Strepsirhini.

By contrast, there have been a number of important developments concerning omomyids in recent years, and the authors involved have tended to support a link between omomyids and tarsiers. One interesting development has been identification of a reasonably complete skull of *Microchoerus* from the Eocene of France<sup>84</sup>. This skull had long been allocated to the closely related genus *Necrolemur*, which is documented by several skulls. The orbits of *Microchoerus* are somewhat larger than in *Necrolemur* and the upper dental arcade does not clearly show the bell shape typically found in other European omomyids. Postcranially, the European omomyids *Necrolemur* and *Microchoerus* differ from the North American forms in having far greater elongation of the anterior segment of the calcaneus<sup>85</sup>, representing a development toward the condition found in modern bushbabies and tarsiers. It has also been claimed that the European forms *Necrolemur* and *Nannopithecus* specifically resemble modern tarsiers in showing distal fusion between the tibia and fibula, although the evidence for *Nannopithecus* has not stood up to closer examination and that for *Necrolemur* is questionable (P. Schmid, personal communication). Rosenberger and Dagosto<sup>84</sup>, however, emphasize apparent derived features of the jaw joint and skull base shared by tarsiers and the European omomyids (Microchoerinae), concluding that there is a specific link between them and that the simians arose from less specialized North American omomyids (anaptomorphines or omomyines). This follows the general trend of inferring a specific link between tarsiers and microchoerines, which were in fact included in the Family Tarsiidae by Simons<sup>86</sup>.

More dramatic was the discovery of four new skulls of the North American omomyid *Shoshonius*, previously documented only by fragmentary jaws and teeth<sup>87,88</sup>. Previously, the skull of Eocene omomyids from North America was known only from an incomplete cranial specimen of *Tetonius*, so the new skulls are in any case of great importance for our understanding of early omomyids. According to Beard *et al.*<sup>87</sup>, however, the skulls

of *Shoshonius* are of special significance because some features, not found in other omomyids, indicate a direct relationship to modern *Tarsius*. This would simultaneously confirm the derivation of tarsiers from omomyid stock, although from omomyines rather than microchoerines, and would push the time of origin of omomyids well back into the Palaeocene. *Shoshonius* resembles tarsiers in having relatively very large orbits, in having a very short snout and in a number of specific features of the ear region. These resemblances are all rather limited, however, and could have arisen through convergent evolution. The possibility of a specific relationship between *Shoshonius* and *Tarsius* could be tested with postcranial evidence. If, for instance, *Shoshonius* were found to show fusion of the tibia and fibula and the same peculiar adaptation of the ankle region as in *Tarsius*<sup>89</sup>, this would provide more convincing evidence of a specific link between these two genera. Postcranial elements and additional skull material of *Shoshonius* have been found, so more information should be forthcoming. At present, the interpretation of omomyid relationships remains confused, with several possibilities still open. On the basis of isolated cheek teeth, the late Paleocene *Altiaflasius* from Morocco has been interpreted as an early omomyid<sup>90</sup>, perhaps indicating an African connection.

## Early simian primates

Until recently, it was often inferred that simian primates (Anthropoidea) first emerged close to the boundary between the Eocene and the Oligocene, just over 35 million years (Myr) ago<sup>1</sup>. The earliest known undoubted simians had been recovered from the Fayum deposits in Egypt, the best-documented genus being *Aegyptopithecus*, which exhibits numerous simian features in the skull and postcranial skeletons. A middle Oligocene age was originally accepted for the Fayum deposits, but subsequently the date was revised to lower Oligocene age<sup>91</sup>. Although it has now been suggested that the entire sequence of the Fayum deposits should be dated as late Eocene<sup>92</sup>, palaeomagnetic reversal stratigraphy indicates that they straddle the Eocene-Oligocene boundary<sup>93</sup>. Even this, however, would indicate an earlier date for the common ancestry of the Fayum simians. Identification of five new fossil simian genera very low down in the deposits (largely based on fragmentary specimens, but including the relatively well preserved skull of *Catopithecus*<sup>94,97</sup>) have reinforced the effects of this redating to indicate that simians must have emerged by the late Eocene, if not earlier. The new discoveries have raised the total number of simian genera reported from the Fayum to 11 (*Aegyptopithecus*, *Apidium*, *Arsinoea*, *Catopithecus*, *Oligopithecus*, *Parapithecus*, *Plesiopithecus*, *Propithecus*, *Proteopithecus*, *Qatrania*, *Serapia*), indicating that considerable diversification had taken place at an early stage. One of the new early forms (*Plesiopithecus*) may have lacked incisors in the lower jaw. If the identification of *Plesiopithecus* as a simian on the basis of a single lower jaw fragment is correct, considerable diversity had apparently already developed following divergence from ancestral simians. On the basis of isolated teeth, simians have also now been reported from earliest Oligocene deposits in Oman (including *Oligopithecus*)<sup>98</sup> and from late Eocene deposits in Algeria (*Biretia*)<sup>99</sup>.

Indications of an earlier date for the Fayum simians may have been superseded by the recovery of dental specimens representing an apparent simian, *Algeripithecus minutus*, from the Algerian site of Glib Zegdou, which is of middle or even early Eocene age<sup>100</sup>. The find is unfortunately confined to three cheek teeth, but the upper and lower molars exhibit a number of simian-like features. In particular, certain upper molar features are shared with *Aegyptopithecus* from the Fayum deposits. If these features are indicative of a sister-group relationship between *Algeripithecus* and *Aegyptopithecus*, as proposed<sup>11</sup>, then the origin of known simians must be pushed back to the lower Eocene or even into the Palaeocene. Against this background,

the late Eocene *Amphipithecus*<sup>101</sup> and *Pondaungia*<sup>102</sup> from Burma clearly now deserve serious re-examination. Both of these fossil genera are of uncertain status but could well be linked to simian origins<sup>103</sup>. Overall, a date of at least 55 Myr instead of just over 35 Myr for the origin of simians now seems possible. It is, in fact, predictable that the simians originated far earlier than hitherto accepted by most authors (See Box 1) and an even earlier date for simian ancestry cannot be ruled out. Nevertheless, although it now seems quite probable that the simian primates emerged much earlier than previously believed, their origins remain obscure (Box 2).

## Future developments

It is clear that there are still many uncertainties regarding the course and timing of early primate evolution. There are, however, several indications that conclusions drawn from an exploratory assessment of the sampling density of the primate fossil record (Box 1) are correct in principle. Our current sample of the primate fossil record is very limited and it follows from this that times of divergence within the primate tree may have been commonly underestimated by a considerable margin. Against this background, it would not be surprising if the time of origin of simian primates were to be pushed back into the Palaeocene, in which case direct migration of simians between Africa and South America<sup>103</sup> becomes far more likely. Limited sampling of the fossil record, combined with the fragmentary nature of most of the fossils concerned, also explains why interpretations of primate evolution have been subject to repeated, often extensive revision. In the face of major gaps in the fossil record, far-reaching interpretation of fragmentary fossil remains can easily lead to misinterpretation of phylogenetic relationships. As a general rule, there has been a tendency to overlook the significance of convergent evolution in the interpretation of fossil primates. If only a limited number of characters can be investigated, it is extremely difficult to test for possible convergence. Greater caution in the interpretation of fragmentary fossil specimens combined with a healthy respect for convergent evolution might help to reduce the level of misinterpretation in the future.

Recognition of the implications of the low sampling level of the primate fossil record in fact raises a new possibility with respect to the evolutionary relationships of the early Tertiary adapids and omomyids. At present, modern strepsirhines, tarsiers and simians have been traced back to adapids or omomyids because these are the only known fossil forms. Rather than seeking to establish direct links with modern primate groups, we should perhaps consider the possibility that the adapids and omomyids together are the outcome of an entirely separate radiation of early primates of modern aspect in the Northern Hemisphere. The divergence between adapids and omomyids could have evolved in parallel to a divergence between strepsirhine and haplorhine primates in the Southern Hemisphere, such that adapids and omomyids are in fact more closely related to one another than to any modern primates. Such an interpretation, which (like all of the potential solutions reviewed above) requires acceptance of a certain amount of convergent evolution, could explain certain features that clash with reconstructions linking adapids to modern strepsirhines and omomyids to modern haplorhines or with alternative hypotheses. It is, for instance, unusual that the adapids were typically larger than omomyids, whereas the reverse is the case for the comparison of modern strepsirhines with haplorhines<sup>104</sup>. Adapids were presumably predominantly diurnal and yet supposedly gave rise to the primary nocturnal strepsirhines, whereas the omomyids were presumably predominantly nocturnal and yet supposedly gave rise to the primarily diurnal haplorhines<sup>14</sup>. As with many other aspects of early primate evolution, more precise answers depend on a continuing, vital effort by field palaeontologists, who will hopefully uncover many more unknown extinct primate species.

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